

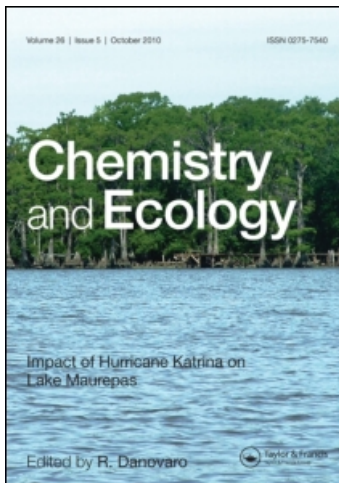
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Chemistry in Ecology: An Editorial Review

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INTRODUCTION

At a time when scientists contribute to and, at times, seem likely to be overwhelmed by an information explosion, one might pardonably question the need for another journal; particularly another journal of an ecological nature. Too often, however, land, sea and fresh water are treated as if they do not interact, and chemistry, although a driving force in ecological systems, is either viewed as an impact upon parts rather than the whole system, or ignored completely: an attitude which is the despair of chemists and a grave loss to ecologists. Indeed, it would seem, particularly in the marine field, that biologists/ecologists are falling far behind the chemists and this is a loss to the scientific community as a whole. One outcome is a lack of the wider view and those attempts to theorise which are necessary to progress in the subject. While not forgetting that an understanding of the component parts is vital to an understanding of the whole, *Chemistry in Ecology* will seek to promote the wider view, and in so doing try to create "bridges" between studies which have not been allied hitherto, but may advantageously work together in the future.

To this end, the journal will seek those papers which although written by ecologists will indicate to chemists those questions that require answers if the ecologist is to make further progress in that area, and *vice-versa*. Thus, in aquatic toxicology, for example, much of the experimentation is concerned with concentration rather than dose, but even of the former little is known either of the chemical species present or of the amount which is truly available to act as a toxin. Yet again little is known of the influence of the organic substances present in water upon the toxicity of added agents though the work of Millward and Burton (1975), Mantoura *et al.* (1978) and

Toledo *et al.* (1980) is indicative of their importance. In the Kilcreggan laboratory, we have for some years been troubled by a poor water quality during the summer when *Asterias rubens*, in particular, has been difficult to maintain (Perkins, 1981); at these times, there appears to be an antagonistic reaction with F^- when introduced as Na_2SiF_6 . In toxicity studies upon effluents, intra-effluent chemistry is not normally a matter for consideration, but the work of Abbott and Perkins (1979) indicates an intrinsically fertile field of investigation, as does the work of Anraku and Kozasa (1978) upon power station effluents. Aquatic toxicology is often viewed as a very poor relation of medical and veterinary toxicology, but in the absence of firm answers to such problems how can it be otherwise?

It is, of course, impossible that the first number of any journal can cover the whole of its intended scope, though it can indicate its breadth. In this respect parasitology and the incidence of disease is rarely included within ecological studies, but as Price (1980) stated "The importance of disease, for example, in big game animals and man, should make us wary of any population study on animals or plants, or any theory on population dynamics, that does not include the parasite-disease complex", a view which the journal is happy to espouse. It is for this reason that papers relating to this aspect will find their place, the papers otherwise are more obviously illustrative of the intended scope and format of the journal.

To emphasise the wider aspect a two part review concerned with the interactions of air, land and water and non-predatory relationships follow; these reviews are not exhaustive, but they do, it is believed, indicate areas of future interest.

INTERACTIONS BETWEEN AIR, LAND AND WATER

The effects of anthropogenic introductions to air, land and water, treated as separate systems, have long been a source of concern as the massive literature testifies. More recently, however, the influence of interactions between either two or three of these major environmental components has become a stimulus for fruitful investigation and international dispute; both indicating that a more integrated view of the world is essential if the problems created are to be understood and solved.

Thus, the atmospheric transport of pollutants be they sulphur dioxide, trace metals or organics, including pesticides, leads eventually to precipitation in rain or snow at situations far removed from their source, often in places not immediately subject to waste input, e.g. the Greenland Ice Sheet (Heron *et al.*, 1977). The result has been an understandable pre-

occupation with the contamination of the land (e.g. Bolin, 1979; Swanson and Johnson, 1980; Evans *et al.*, 1980), fresh waters (e.g. Holden, 1966; Elgmork *et al.*, 1973; Hagen and Langland, 1973; Velds, 1974; Forland and Gjessing, 1975; Gatz, 1975; Chassaing, 1976; Versino *et al.*, 1978; Delisle *et al.*, 1979; Scheider *et al.*, 1979; Evans *et al.*, 1980; Lynch and Corbett, 1980; Kortmann, 1980) and the sea (e.g. Duce, 1978; Berg and Winchester, 1978; Gravenhorst, 1978; Harder *et al.*, 1980) by atmospheric pollutants and, in some measure, with the ecological consequences. Of the papers listed, two seem to have outstanding implications for the ecologist: that by Swanson and Johnson (1980) showed how Cd, Cu, Fe, Mn, Ni and Pb are accumulated in the forest by bulk precipitation, but whereas Cu, Ni and Pb are accumulated in the forest ecosystem, the Fe and Mn complex with mobile organic matter and are thereby lost. On the other hand, Harder *et al.* (1980) showed that the input of toxaphene by rainfall to a South Carolina estuary was approximately 0.5 kg km^{-2} in 4 months, exceeding by some 10 to 100 times that of P.C.B. and D.D.T. While these are the facts, as reported, the argument can, however, be carried much further, for once in water many substances, including chlorinated hydrocarbons, become adsorbed upon the suspended solids—inorganic and organic—and sediments (e.g. Choi and Chen, 1976; Jonas and Pfaender, 1976; Hannan and Thompson, 1977; Hiraizumi *et al.*, 1979) and, thence transported with them by normal hydrological processes. Thus the work of Gallagher *et al.* (1979) suggests that coastal and estuarine hydrography (e.g. see Perkins, 1974) may play a dominant, though not exclusive role in the accumulation of toxaphene in salt marshes, since it is accumulated particularly at those levels flooded daily by the tide and only slightly at higher levels. This is consistent with the work of Perkins and Williams (1966) upon the transport of ^{106}Ru and $^{95}\text{Zr}/^{95}\text{Nb}$ from the Irish Sea and their deposition in the Solway Firth. Here, the intra-estuarine processes of input, reworking and deposition by tidal currents masked the influence of the rivers and the direct input of fall-out in rain could be recognised only on the grass marshes and those algae, viz., *Fucus spiralis* and *Pelvetia canaliculata* which lived at levels above the lowest high water mark of neap tides (L.H.W.M.N.T.)(Williams and Perkins, 1965).

Returning now to the pesticides, an estuarine burden, E.B., depends upon the following interaction

$$E.B. = F_w + R_d + R_f - B_d - B_i - H_i$$

where

B_d = that lost by biological degradation (e.g. Alexander, 1974).

B_i = that lost by biological transport either by migration or loss of litter and detritus,

F_w = that introduced by the rivers (e.g. Likums, 1979),

H_i = that lost by hydrographic transport in periods of exceptional river flow,

R_d = that introduced by rain falling directly on the estuary,

and

R_i = that introduced by suspended solids which have adsorbed the pesticide after rain has fallen upon coastal waters.

Clearly, the relative value of each will influence the final value of the estuarine burden, E.B., which will tend to be individual to the estuary. Not least, since the relative sizes of the catchment area and the estuary fundamentally influence its hydrography (e.g. see Perkins, 1974), the relative direct impact of rainfall and total biota available for participation in the processes of transport and deterioration.

This model, while indicating that the processes which should be recognised and understood for a balanced view of this problem, implies that the sea and in particular the estuary is a long term, if not final, repository for these materials. Indeed, this is a general view implicit in the many processes of waste disposal to the sea by outfall or dumping from ships and where, in effect, the philosophy of dilution and dispersion prevails. This has, of course, been a useful, pragmatic approach to an otherwise difficult problem, but it might be worthwhile to consider its validity, particularly for releases made between the high water mark and for some hundred metres to the seawards of the low water mark.

The transfer of air pollution by the global atmospheric circulation and its eventual deposition in the aquatic environment is merely one important aspect of aerosol chemistry. Another aspect is concerned with the transport of dust, thus substantial amounts from north west Africa and the Sahara Desert may be deposited on the Algarve coast of Portugal (Schmidt *et al.*, 1978), the Cape Verde Islands (Jaenicke and Schutz, 1978), the Atlantic Ocean (Szekielda, 1978; Prospero *et al.*, 1981), northern Europe and South America (Prospero *et al.*, 1981). Regarding the movement of dust out over the Atlantic from Africa, Prospero *et al.* (1981) considered that the amount being transported is of the order of 100–400 megatonnes (where 1 megatonne = 10^{12} g) per year. While some of this material reaches South America, some 4,000 km distant, in 4–5 days and there influences the climate, it provides a very substantial fraction of the non-biogenic material entering the deep-sea sediments in the tropical and equatorial Atlantic. Szekielda

(1978) noted that samples of such eolian dust may contain *Actinomyces* and other microorganisms, but Prospero *et al.* (1981) found no readily identifiable biological material in Sahara dust arriving at Cayenne, French Guiana, although the diameter of the dust particles, 20 μm , was similar to that of many fungal spores.

No less important, however, is the transport of aerosols marine in origin arising as spray which fails to return to the sea and subsequently evaporates to produce salt nuclei. Even in 1952 Carson noted that 26.9 to 40.4 $\text{kg ha}^{-1}\text{yr}^{-1}$ of salts from such an origin fell on England while Sambhar Salt Lake in northern India received 3,000 tons yr^{-1} by this means. It is now considered that some 2×10^9 tons of salt passes through the whole world atmosphere annually (e.g. Ericksson, 1959; Woodcock, 1962). The chemistry is complex and the marine aerosol may not have the same composition as sea water since some ions are relatively enriched and others are relatively impoverished (e.g. Holden, 1966; Malloch, 1972; Paterson and Scorer, 1975; Zafirou, 1975; Cattell and Scott, 1978; Graham *et al.*, 1979). In addition to inorganic salts, the marine aerosol may contain nutrients, organic substances, bacteria and viruses (Woodcock, 1948, 1955; Wilson, 1959; Aubert, 1972, 1976; Aubert and Bely, 1977; Blanchard, 1978).

In a sense, the foregoing can be considered a rather straightforward manifestation of the interrelationships between sea, land and air. There are, however, rather less obvious phenomena whose implications have been neglected, but which *a priori* are of such importance that they ought not to be excluded from considerations of environmental management. Thus in those estuaries and inshore areas which are adjacent to large industrial installations, e.g. oil refineries and power stations, or towns which emit large amounts of SO_2 industrial hazes are often present, e.g. Teeside. These hazes result when ammonia which passes from the sea surface to the atmosphere reacts with the water vapour and the SO_2 to form ammonium sulphate (Eggleton, 1969). Since the nitrogen content of sewage is some 50–75% NH_3 (Klein, 1969), it might appear that the NH_3 derives from this source even though sewage is >99% water. However, NH_3 is a principal component of the nitrogenous waste excreted by most aquatic animals (e.g. Srna and Baggaley, 1976; Rychly and Marina, 1977; Ikeda and Motoda, 1978; Mangum *et al.*, 1978; Roger, 1978; Smith, 1978; Chin and Lee, 1979; Lewin *et al.*, 1979; Regnault, 1979; Gerhardt, 1980; Lehmann, 1980; Crisp *et al.*, 1981; Tátrai, 1981) and may be produced by excretion from or decay of phytoplankton blooms (Le Borgne, 1978). Using the data of Roger (1978) and Raymond (1972), for example, it can be shown that the rates of loss of NH_3 to the atmosphere reported by Weiler (1979) may be satisfied by these means, though not excluding the possibility that sewage may

contribute to it. Here then the presumption of dilute and disperse, viz., SO_2 in the atmosphere, while broadly true fails, at least in the local sense, because of the normal emission of the volatile NH_3 from the surface of the nearby sea. Thus, two aerosols, very different in origin, produce a third whose ecological effects are, I believe, largely unexplored.

While the role of sewage in the foregoing relationship is uncertain, it also contains other materials including pathogenic organisms which may be returned to the land by seagulls (e.g. Silverman and Griffiths, 1955; Wuthe, 1972). However, even 40 yr. ago ZoBell (1942) recognised that micro-organisms might be transported in the marine aerosol, and while Woodcock (1955, 1962) and Blanchard (1978) showed that bacteria and viruses might become airborne in droplets, it remained for Aubert (1972, 1976) and Aubert and Bely (1977) to point out that nannoplankton, diatoms dinoflagellates, terrestrial bacteria and mildews may be similarly transported to influence marine and supralittoral ecology. Most sewage released to the sea undergoes little treatment, other than comminution to reduce its size (and immediate aesthetic impact), thus the inhabitants of an exposed coast, are exposed to some public health risk (Aubert *et al.*, 1979). They, the sewers transporting their sewage and the adjacent sea represent three components in a disposal system in which the concept of dilute and disperse is only partially true.

What of the other effluents, of great variety, which are released to the sea having undergone little or no treatment? The work of Huhnerfus *et al.*, (1977) and Blanchard (1978) suggest both normal biological processes and the quality of waste disposal might influence aerosol transport from sea to land. The literature seems to have little to offer, although the work of Klug (1973), Whelan (1975) and Hitchcock *et al.* (1980) indicate clearly that coastal and island sites receive substantial amounts of salt from the sea, and therefore, by inference, one might expect that wastes released between the E.H.W.M.S.T. and the immediate sub-littoral might be deposited on the coastal lands in significant amounts. In one such problem of which I am aware, the chemical works concerned releases effluent at the low water mark. In a study of the deposition of air-borne solids at a number of stations, it was found, not unexpectedly, the wind was an important factor in the deposition, but since everyone tends to compartmentalise the different aspects of a problem, the possibility of a contribution from the sea had been overlooked. However, the occurrence of chloride, in particular, indicated a strong marine influence in the deposits so that the marine aerosol contribution of this waste to the land cannot be ignored and its magnitude is being assessed. A clear implication derives from this, viz., although one may dispose of waste to the aquatic environment, it is not that environment alone which should be monitored carefully.

The interesting work of Harrison (1981) presents another aspect of this problem, for in his studies of the distribution of tetra-alkyl lead compounds in the air of north-west England, he found that a significant amount has a marine origin. Clearly, the problem posed by the use of these substances in petrol is no longer as simple as it once seemed.

Alternatively, it might be more useful to reconsider our definitions relating to the marine environment, more especially that of the splash zone or supralittoral fringe which is generally considered to be a rather narrow zone above the E.H.W.M.S.T., extended vertically in those situations exposed to severe wave action (e.g. Perkins, 1974). In the latter, zonation of the marine inhabitants is extended substantially above the E.H.W.M.S.T., and cliffs upwards of 100m. in height are abundantly colonised by lichens, e.g. *Xanthoria*, *Caloplaca*, *Lecanora* and *Ochrolechia*, on the more exposed surfaces and halophytes in those situations which permit a root hold. I would draw particular attention to the lichens, for examination of buildings adjacent to the coast and for some distance inland indicates that they are colonised by the splash-zone species. Thus on Solway Coast, for example, roof and wall are colonised predominantly by *Xanthoria/Caloplaca* and *Lecanora/Orcholechia* respectively; the colonisation, although influenced by the quality of the surface colonised, appears to be most abundant on the seaward side of buildings and with increasing proximity to the sea. Inland, the grey lichens become more dominant overall and mosses become increasingly important. Using the lichens as indicators, it seems reasonable to propose that the direct ecological impact of the splash zone may be experienced by the inhabitants of rock-like substrata for some kilometres inland; as it is indeed by the largest rooted plants and trees (e.g. Malloch, 1971; Potts, 1978). The response as one might expect is graduated, but so far as I am aware there are few recent ecological studies of these substrata. Clearly a roof is not easy of access, but this does eliminate other variables such as continuous human impact. Moreover, the work of Wilson (1959) upon the marine aerosol as a source of nitrogenous and other nutrients and that of Morgan (1977) upon the tardigrades *Macrobiotus hufelandii* and *Echiniscus (E) testudo* inhabiting roof mosses in Swansea indicates plainly the valuable insight into the ecological effect of marine aerosols which may be gained by such studies: here too, surely, marine and xerobiology have common features worthy of investigation.

NON-PREDATORY RELATIONSHIPS

Although, the hypothesis that organic matter dissolved in sea water offers a significant source of food to aquatic organisms postulated by Pütter (1909)

was firmly rejected by Krogh (1931), Pütter's insight has since been vindicated by the development of an exciting and far reaching aspect of aquatic biology. Though, no doubt, much of what has happened since 1931 far exceeds the vision of that perceptive man. It was, however, Lucas (1947, 1955, 1961) who set the present course by formulating the theory of non-predatory relationships which states that in its life-time an organism, plant or animal, secretes organic materials which may be of advantage or disadvantage to associated organisms. Where these substances are of advantage they may be growth factors, or may act as a trigger influencing behaviour and ecological equilibria: such substances acting at sites remote from the source may be referred to as chemical telemiators (e.g. Aubert, 1978). Conversely, some secretions may be disadvantageous as is the case with red tides and paralytic shellfish poisoning (e.g. Dale and Yentsch, 1978). Work such as that by Ryther, 1954; Carpenter *et al.* (1972), Uchida (1975), Ikeda and Motoda (1978), Liao and Lean (1978), Smith (1978), Lewin *et al.* (1979), Turner (1979) and Lehmann (1980) demonstrating the utilization of ammonia, urea and uric acid, all nitrogenous wastes from animals, by bacteria, planktonic algae and phaeophytes, or that of McRoy and Barsdale (1970), McRoy *et al.* (1972), Reimold (1972), Axelrad *et al.* (1974), Valiela *et al.* (1978) and Burns and Taylor (1979) relating to the cycling of phosphorus by halophytic grasses and that of Bartolecci *et al.* (1978) upon the release of phosphate into soil by algae, suggests that a discussion of external metabolites and non predatory relationships solely in terms of organic secretions may be too narrow a view.

In addition to these substances, a wide variety are derived from many organisms thus hydroxylamine is secreted by bacteria and algae (e.g. Berger *et al.*, 1979; Hanusova and Havlik, 1979), fatty acids and lipids (including sterols which Morris and Culkin (1977) noted are present in many organisms) by bacteria, phytoflagellates, bivalves and fish (e.g. Billmire and Aaronson, 1976; Teshima and Kanazawa, 1978; Yano and Ishio, 1978; Gauthier *et al.*, 1978; Halvorson and Martin, 1980), glycollic acid and glycollates by algae (e.g. Wright and Shah, 1975; Bolze and Soeder, 1978; Colman, 1978), carbohydrates by algae, nannoplankton, diatoms and fish (Marshall and Orr, 1962, 1964; Marker, 1965; Williams *et al.*, 1974; Bolze and Soeder, 1978; Vogel *et al.*, 1978; Mague *et al.*, 1980), peptides by algae (e.g. Bolze and Soeder, 1978), amino acids by blue-green algae, algae, bivalve molluscs and fish (e.g. Stewart and Pugh, 1963; Jones and Stewart, 1969a; Williams *et al.*, 1974; Vogel *et al.*, 1978; Chin and Lee, 1979; Mohan and Mukerji, 1979), polyphenols by fucoïd algae (e.g. Ragan and Jensen, 1978, 1979), vitamins by blue-green algae (e.g. Jones and Stewart, 1969b), hormones by blue-green algae (e.g. Mohan and Mukerji, 1979), inhibitors by blue-green algae, algae and dinoflagellates (e.g. Gauthier *et al.*, 1978;

Honjo *et al.*, 1978; Berger *et al.*, 1979; Mohan and Mukerji, 1979; Herrera and Martin, 1980); antibiotics by algae, diatoms and bryozoans (e.g. Al-Ogily and Knight-Jones, 1977; Gauthier *et al.* 1978, 1980), pheromones and attractants by lamellibranch molluscs and fish (e.g. Hidu *et al.*, 1978; Morse *et al.*, 1979; Derby and Atema, 1980; Selset and Doving, 1980), cytolytic and neurotoxic agents by blue-green algae and dinoflagellates (e.g. Dale and Yentsch, 1978; Eng-Wilmot and Martin, 1979; McCoy *et al.*, 1979; Moon and Martin, 1979; Halvorson and Martin, 1980), and allergens by blue-green algae and bryozoans (e.g. Audebert and Lamoureux, 1978; Solomon and Stoughton, 1978). Of these sources, perhaps the best understood is the process of nitrogen fixation by bacteria and blue-green algae (Wicks, 1974; Stewart and Pugh, 1963; Jones and Stewart, 1969a, b; Bharati and Bongale, 1976; Bohlool, 1978; Carpenter *et al.*, 1978; Feige and Ritschel, 1978; Finke and Seeley, 1978; Moeller and Roskoski, 1978; Gotto *et al.*, 1979; Horne, 1979; Horne *et al.*, 1979; Mohan and Mukerji, 1979; Potts, 1979; Sakevich *et al.*, 1979; Zuberer and Silver, 1979) and while nitrogen fixing organisms are widely distributed in fresh waters, it is the salt marshes and mangrove swamps which are so important as the habitat of these organisms in the sea (e.g. Carpenter *et al.*, 1978; Potts, 1979). According to Bharati and Bongale (1976) blue-green algae may release as much as 32 to 40% of the nitrogen fixed to the medium and Feige and Ritschel (1978) state that blue-green algae are of such an important factor in the nitrogen cycle that they contribute an estimated 40×10^6 tonnes to the marine ecosystem per year; in total, the biosphere releases to the environment an estimated 175×10^{10} tonnes of such combined nitrogen which is approximately 6 times the annual industrial production of fertilisers.

Although plant and animal excretions supply substantial amounts of dissolved organic substances, they may also be released from cells broken during grazing (e.g. Lampert, 1978), by leakage across the animal epidermis (e.g. Pechenik, 1979) and the breakdown of tissues after death; even the manner in which experimentation is performed may lead to false conclusions and controversy (e.g. Aaronson, 1978; Sharp, 1978; Shimura *et al.*, 1978). To consuming organisms the mode of origin is a matter of indifference, for it is the availability of these substances which is vital to their well-being and survival. Currently, the number of surveys reported and the results obtained are indicative of a growing awareness of the importance of these substances and the variety and quantity in which they are present in water (e.g. Clark *et al.*, 1972; Ohwada and Taga, 1972; Zlobin *et al.*, 1975; Gagosian, 1977; Kurelec *et al.*, 1977; Bruno and Staher, 1978; Daumas, 1978; Dawson and Gocke, 1978; Nishijima and Hata, 1978; Mel'nikov and Pavlov, 1978; Perkins, 1978; Solorzano, 1978; Gardner and Hanson, 1979; de Haan and de Boer, 1979; Inoue, 1979; Kabori and Taga, 1979; Naletova, 1979; Nishijima and Hata, 1979).

While it is recognised that there is a general requirement by living organisms for the metabolic products of others (e.g. Williams *et al.*, 1976; Boutry, 1978; Hanson and Gardner, 1978) much is also known of the absorption and utilisation of these substances by particular groups or species. Thus in addition to utilisation of nitrogenous wastes noted above amino acids which may be important in chemoreception (e.g. Carr, 1978; Goh and Tamara, 1980) and induction of larval settlement (e.g. Morse *et al.*, 1979), are absorbed and utilized by microflora (e.g. Berland and Bonin, 1976; Dawson and Gocke, 1978), flagellates (e.g. Ryther, 1954; Droop, 1957, 1958; Pinter and Provasoli, 1963; Turner, 1979), dinoflagellates (e.g. Uchida, 1975), chlorophytes (e.g. Jones and Stewart, 1969b; Kirk and Kirk, 1978; Smith and Gayler, 1979; Turner, 1979), diatoms (e.g. Corrigan and McLean, 1979; Turner, 1979), halophytes (e.g. Cavalieri and Huang, 1979), coelenterates (e.g. Schlichter, 1976), annelid worms (e.g. Siebers and Ehlers, 1978; Costopulos *et al.*, 1979), bivalve molluscs (e.g. Sansone *et al.*, 1978; Wright and Stephen, 1978; Elliott, 1979; Stewart and Dean, 1980), pogonophorans (Southward *et al.*, 1979), *Phoronis* (Emig and Thouveny, 1976), echinoderms (e.g. Pavillon, 1976; de Burgh, 1978); methylamine a product of amino acid decarboxylation and the decomposition of fish is absorbed by the phaeophyte *Macrocystis pyrifera* (Wheeler, 1979); other organic acids, lipids and sterols by microflora (e.g. Cahet, 1974, 1975; Wright and Shah, 1975; Coughlan and Al-Hasan, 1977), coelenterates (e.g. Saliot, 1976), lamellibranch molluscs (e.g. Saliot, 1976; Bunde and Fried, 1978); carbohydrates by microbial organisms (e.g. Berland and Bonin, 1976; Christian and Wiebe, 1978; Robarts, 1979), chlorophytes (e.g. Prazukin, 1978), rhodophytes (e.g. Prazukin, 1978), flagellates (e.g. Robarts, 1979), dinoflagellates (e.g. Robarts, 1979), brachipods (e.g. McCammon and Reynolds, 1976), copepods (e.g. Khailov and Erokhin, 1971; Swift *et al.*, 1975; Gryllenberg and Lindqvist, 1978), and pogonophorans (Southward *et al.*, 1979); vitamins by flagellates (e.g. Droop, 1958, 1959, 1961; Cantor, 1978; Turner, 1979), Chlorophyta (e.g. Moss, 1973; Turner, 1979), dinoflagellates (e.g. Uchida, 1975; Turner, 1979), diatoms (e.g. Moss, 1973; Swift and Guillard, 1978; Turner, 1979) and echinoderms (Pavillon, 1976); macrophytic algal exudate by lamellibranchs (e.g. Fankboner and de Burgh, 1978; Fankboner *et al.*, 1978); glycerophosphates by dinoflagellates (Uchida, 1975) and gibberellic acid by blue-green algae and diatoms (Ramamurthy, 1976).

Such a bald list implies an essentially simple relationship between the external metabolite and its uptake by a particular organism, though the reality may be more complex. Thus the starfish *Echinaster* can ingest and assimilate dissolved amino acids, but it is not dependent upon this source of food (Ferguson, 1979, 1980); furthermore, Sieburg (1979) showed that

while bacteria were involved in the uptake *Asterias rubens* is not dependent upon this source of food. Apparently such bacteria are also important in the uptake of hexoses by penaeid shrimp postlarvae (Castille and Lawrence, 1979). It might be considered that in lacking a gut the pogonophorans are likely to be dependent directly upon the dissolved organic matter in sea water as a source of food, but as Southward *et al.* (1979) have shown the immediate environment of *Siboglinum fiordicum* must be richer in amino acids and glucose than the analyses of interstitial water would imply, i.e. if the metabolic needs of *Siboglinum* are to be satisfied; consequently they suggested the possibility that the pogonophores utilise the metabolic products of associated microorganisms and/or anaerobic animals. While Sepers (1977) suggested, and Southward *et al.* (1979) noted that, the microorganisms may not be associates so much as competitors for dissolved organic matter, Cahet (1974) found the microflora to possess the necessary metabolic adaptation whereby the organic acid reserve which is so strongly bound to sediments may be utilised. While Cahet's results would seem to favour an association, should the relationship be competitive as Sepers (1977) suggested, then it is implicit that *Siboglinum* itself can break down this binding with the sediment. Whichever is true, the outcome of these studies is clearly a matter of considerable interest.

Although *Siboglinum* cannot apparently satisfy all its metabolic requirements from the organic substances dissolved in its environmental water, nevertheless larva and adult can meet 54 and 73% respectively of their requirements from this source (Southward *et al.*, 1979); similarly the sea anemone *Anemonia sulcata* can meet a substantial proportion of its metabolic requirements in this way (Schlichter, 1974) and according to Fankboner (1976) the absorption of dissolved organic carbon from seawater may be critical to the survival of the coral *Balanophyllia elegans* during the winter when its normal zooplanktonic food supply is insufficient. The harpacticoid copepod *Tigriopus brevicornis* can meet 13% of its total ration by the sorption of mono- and polysaccharides from sea water, but in this respect *Calanus finmarchicus* (1.2% of ration so accumulated) is much less effective (Khailov and Erokhin, 1971) and it was, of course, Morris (1955) whose studies of fish larval nutrition that gave an impetus towards these later studies.

Thus far the discussion has been confined to the uptake of organic substances from an unspecified source and those cases where bacteria have either facilitated such uptake or an association is implied. There are, however, cases in which the association is close and in which a metabolite passes from one associate to the other. Thus a *Zoogloea* sp. of bacterium lives attached to the blue-green alga *Anabaena flos-aquae* (Caldwell and Caldwell, 1978); nitrogen is transferred from blue-green algae to grasses in

sand dune slacks (Stewart, 1967); nitrogenous nutrients are transferred from soil to its epiphytes by *Zostera marina* (McRoy and Goering, 1974) and the epizoitic bryozoan *Membranipora membranacea* derives nutritional benefit from exudate of the host kelp *Nereocystis luetkeana* (de Burgh and Fankboner, 1978). While these relationships are symbiotic, the association between the donor and receptor organisms are essentially a matter of degree, for in these cases the transfer is direct and there is effectively no transport by water between the two organisms. Such observations coupled with those of Castille and Lawrence (1979), Siebers (1979) and the suggestion by Southward *et al.* (1979) that the pogonophores may be dependent upon the metabolic products of associated organisms lead one to speculate that such associations might be widespread in the aquatic environment.

A curious relationship is displayed by the nudibranch molluscs which utilise the metabolites of prey organisms in their own mucous secretions as a defense against predators: thus *Aplysia californica* metabolises the toxic brominated sesquiterpenes from *Laurencia* and stores them in its digestive gland and *Doropsilla albopunctata* absorbs an acetylcholine antagonist in its food, and an extract of this will kill shore crabs (Reel and Fuhrman, 1981). This is clearly not a non-predatory relationship, but at the eco-chemical level is effectively indistinguishable from the relationships discussed above and in this respect parasitism is merely the most extreme case of proximity between donor and receptor. Thus the complex media necessary for the culture of parasites (e.g. Bahnweg, 1980), the competition between species of gut parasite for soluble nutrients and the contribution made by the milkweeds to the antibiotic properties of large milkweed bug haemolymph (Price, 1980) are indicative of a chemico-ecological relationship which differs from those of the free-living species only in degree.

Botanists have long realised that repeated growth of some crops leads to diminishing productivity, i.e. "soil sickness", and that volatiles, leaf leachates, root exudates and litter fall may exclude seedlings of the same and other species from sites adjacent to the source plant. The phenomenon is known as allelopathy (e.g. Bonner, 1950; Tukey, 1969, 1970; Newman and Rovira, 1975; Friedmann *et al.*, 1977; Swain, 1977 and Stowe, 1979). The leachates from plants include inorganic nutrients, polysaccharides, hexose and pentose sugars, pectic substances, sugar alcohols, amino and organic acids, gibberellins, carotenoids, coumarins, vitamins, alkaloids, phenolics, glucosinolates, terpenes, steroids and proteins (Tukey, 1970; Swain, 1977). Particular effects noted include the excretion of oxalic acid by the roots of *Oxalis*, substantial quantities of organic and amino acids by legume roots and the inhibitors absinthin by the leaves of *Artemisia absinthum*, 3-acetyl-6-methoxybenzaldehyde by the leaves of *Encelia farinosa* and trans-cinnamic acid by roots of the guyale, *Parthenium*

argentatum. Within the soil, transformation to toxic derivatives may occur, thus the non-toxic 4- β -glucoside of hydrojuglone leached from the leaves and fruit of the walnut, *Juglans regia* is hydrolysed and oxidised to the naphthoquinone juglone which severely inhibits the germination and development of many undergrowth species; similarly, amygdalin exuded by the roots of the peach (*Prunus persica*) is converted to benzaldehyde which inhibits the growth of another tree in the same location (e.g. Bonner, 1950; Tukey, 1969, 1970 and Swain, 1977); moreover as Newman and Miller (1977) showed phosphorus uptake may be influenced both positively and negatively by root exudates. According to Swain (1977) relatively few allelopathic agents have been identified from given ecological situations, few examples of the quantitative effect of individual phytotoxins recorded and the overall picture has been grossly neglected.

Although Starkey (1929) recognised that root exudates might influence soil micro- and macro-organisms, this field has been relatively little studied. Nevertheless, oat and pea root exudates may stimulate the growth of Gram-negative bacteria (Rovira, 1956) and those of grasses inhibit free living nitrifying and nitrate oxidising bacteria (Muller *et al.*, 1966; Munro, 1966), while those of the grass *Aristida adscensionis* inhibit the development of the free-living nitrogen fixing bacterium *Azotobacter*, reduce the number of nodules upon *Indigofera cordifolia* (Murthy and Ravindra, 1974) and inhibit the activity of *Rhizobium* derived from those nodules (Murthy and Nagodra, 1977). In addition to influencing the number and behaviour of soil microorganisms, Tukey (1970) noted that leachates can influence soil texture, aeration, permeability and exchange, hence the soil forming processes, fertility and susceptibility/immunity to soil pests. On the other hand, the nutrient status of the soil can influence the quality of plant litter and leachates: thus application of nitrogen fertiliser to Corsican pine increased the weight of needle fall; the concentrations of N and K in that litter increased, but those of P, Ca and Mg decreased. Conversely the quality of crown leachates was unaffected except for the K release which increased from 3.2 ± 2.8 to 8.5 ± 5.3 kg ha⁻¹yr⁻¹ when the fertiliser applied was raised from 0 to 504 kgN ha⁻¹yr⁻¹ (Miller *et al.*, 1976).

I have been unable to find any work relating to the influence of these substances upon animals though the relationship between animals and the source and abundance of their food supply (e.g. Beyer and Saari, 1977) are indicative of the indirect influence of leaf leachates, litter fall and root exudates upon the fauna. Considering, the known effect of similar substances upon aquatic biota one might infer that litter and soil dwelling animals are influenced by leaf leachates and root exudates. Again, terrestrial botanists have considered essentially local effects, but it seems logical to conclude that a substantial transfer from the soil to adjacent

water courses must occur, particularly in areas of high rainfall: indeed, the role of saltmarsh and sea grasses in "pumping" nutrients into the overlying water is both part of the leaching process and an indication of its likely influence from non-aquatic sources. Clearly forests and mangrove swamps growing along the margins of water courses can make direct contributions of both exudates and leachates which are then available for utilisation and production of aquatic biota. There seems to be no literature concerned with this possible relationship and its consequences, although gibberellins, for example, which occur in leachates (Tukey, 1970) are, according to Ramamurthy (1976) stimulants of blue-green algae and diatoms.

Nevertheless, it can be shown that such relationships may possibly exist widely. The non-protein amino acids present in plants and animals were considered by Swain (1977) to be among the most interesting of the secondary metabolites acting as allelopathic agents, thus azetidine-2-carboxylic acid is a lower homologue of proline and may replace it in the bean, *Phaseolus*. In the aquatic environment, algae secrete amino acids, including proline (e.g. Vogel *et al.*, 1978; Mohan and Mukerji, 1979), and such free amino acids, including glycine, arginine, proline and alanine, comprise some 78.7% and 70–95% of the total amino acid pool of the crustaceans *Carcinus* and *Palaemon* respectively (D'Aniello, 1980); moreover, larvae of the stone crab *Menippe mercenaria* contain twice the concentration of free amino acids when maintained at 40‰ as compared with 20‰ salinity: some, particularly proline, undergo an 8-fold increase in concentration (Tucker, 1978). The cichlid *Saratherodon mossambicus* when presented with a low protein diet grows rapidly by assimilating detrital non-protein amino acids. On the other hand, Raschke *et al.* (1975) concerned with the provision of potable water reported that water from the Broad River, South Carolina had a "musty" or "earthy" smell and a foul taste which was strongest coincident with the highest average concentrations of total organic carbon, $\text{PO}_4 - \text{P}$, $\text{NO}_3 - \text{N}$ and total Kjeldhal nitrogen and the maximum of actinomycete odour; leaf litter odours became stronger as the weight of litter decreased. Clearly, leaf leachates and root exudates are not apparently involved, nevertheless, the principle is clear, viz., leaves fall into the Broad River, from nearby trees, providing a substrate for the actinomycetes which produce organic substances that although obnoxious to humans had clearly conditioned the river, but were of uncertain ecological effect otherwise. Currently there is enormous pressure on the world's forests, particularly mangrove and tropical rain forest, and given the possibilities noted above, it would seem that development of this field of study would be timeous particularly in relation to the world's equally hard pressed fisheries.

That this conclusion is reasonable may be judged on the basis of the

known quantities of leachates produced: thus apple trees (*Malus domestica*) may lose 800 kg. carbohydrate $\text{ha}^{-1}\text{yr}^{-1}$ and up to 6% of the dry weight equivalent, as carbohydrate, can be leached from young bean leaves (*Phaseolus vulgaris*) in 24 h (Tukey, 1970); northern hardwood forest may contribute 115.44 kg organic matter ha^{-1} , 8.13 kg Total N ha^{-1} , 0.63 kg. PO_4 ha^{-1} , and 29.71 kg K ha^{-1} in the growing season from June to October (Eaton *et al.*, 1973) and a red alder (*Alnus rubra*) stand studied by Turner *et al.* (1976) contributed 8.9 kg Total N $\text{ha}^{-1}\text{yr}^{-1}$, 3 kg. PO_4 $\text{ha}^{-1}\text{yr}^{-1}$ and 12.8 kg K $\text{ha}^{-1}\text{yr}^{-1}$. While analyses undertaken vary from worker to worker, there is a generally similar picture evident in the literature even though the amounts vary with habitat and species (e.g. Zamierowski, 1975; Henderson *et al.*, 1977). To this process must be added the enrichment which occurs when leaves are added to the litter (e.g. Ewel, 1976; Henderson *et al.*, 1977; Kellman, 1979) thus the non-leguminous nitrogen fixing woody angiosperms *Hippophaë rhamnoides* (Sea Buckthorn) and *Myrica gale* (Bog Myrtle) contribute up to 180 kg N $\text{ha}^{-1}\text{yr}^{-1}$ and at least 30 kg N $\text{ha}^{-1}\text{yr}^{-1}$ respectively to the soil during the leaf fall (Sprent *et al.*, 1978). Such figures and the inter-specific associations recognised by gardeners suggest that modern agricultural monoculture may be influencing crop quality and thus be worthy of investigation.

Although the foregoing consideration of non-predatory relationships and external metabolites is indicative of effects upon individual species and parts of systems, it does not provide a rounded view of the ecological and economic implications. Perkins (1977) attempted such an approach in the following hypothesis "In situations of high input of nutrient materials—particularly (but not exclusively) those derived from sewage—the salt marshes, by their ability both to use and to transform such materials, act as a safety valve to prevent the development of the unpleasant consequences of red tide in the main water body or excessive green algal growth on sand and mud flats. Where such salt marshes are absent, certain nutrient components associated especially with untreated sewage can, either in the absence of external metabolites derived from salt marshes or in the lack of the mechanism inherent in salt marshes to utilize these materials, promote the development of these symptoms; but in neither case is the ambient concentration of phosphate and nitrate the causative agent." Some 4 years have since passed and an examination of it might be apposite, particularly in view of the widespread occurrence, economic and public health implications of the phenomenon (e.g. Woodcock, 1948; Kim *et al.*, 1976; Dale and Yentsch, 1978; Boalch, 1979; Ottway *et al.*, 1979): indeed, financial losses of the order of $\$5 \times 10^9$ and $\$9 \times 10^9$ have been incurred in fisheries off Florida and in the Seto Sea respectively (Halvorson and Martin, 1980). If the marine wetlands do act as a moderator of this

phenomenon, it would be advisable to balance the alleged advantages of reclamation against such serious losses.

The marine grasses, viz., *Spartina* and *Zostera*, absorb inorganic phosphate through the roots and return it, through the leaves, to the water as dissolved inorganic and organic phosphorus (McRoy and Barsdale, 1970; McRoy *et al.*, 1972; Reimold, 1972; Axelrad *et al.*, 1974; Teal and Valiela, 1978; Welsh, 1980). In Izembek Lagoon, McRoy *et al.* (1972) found that *Zostera* excreted $62.4 \text{ mg P m}^{-2} \text{ day}^{-1}$, i.e. some 37% of that absorbed from the sediment, and of this ca. 41% of the reactive phosphorus or 3 tonnes day^{-1} were exported from the 218 km^2 lagoon to the Bering Sea. Ignoring seasonal fluctuations and assuming an annual export of 540 tonnes reactive P to the Bering Sea, the phosphorus input to the grass may be estimated at 3600 tonnes/yr which is of the same order as the 2,900 tons P yr^{-1} added by London to the Thames Estuary (Carruthers, 1954) which is surrounded by substantial, though diminishing marshes. In a computer simulation of phosphorus loadings of the flood plain marshes of the Kissimmee River, Florida, Burns and Taylor (1979) found that some 50% of the phosphorus loading to $5 \text{ g m}^{-2} \text{ yr}^{-1}$ would be captured permanently by the marsh, and, of that exported, some 90% would be transformed to the detrital state and be unavailable to nuisance algae.

Unlike phosphorus, nitrogen is limiting in the process of marine eutrophication and is fixed particularly, though not exclusively by blue-green algae (e.g. Jones and Stewart, 1969a; Bharati and Bongale, 1976; Bohlool, 1978; Carpenter *et al.*, 1978; Feige and Ritschel, 1978) and takes place over the whole marsh rather than in any one part of it (Jones, 1974). Feige and Ritschel (1978) estimated the amount of combined nitrogen added to the marine ecosystem by blue-green algae to be 40×10^6 tonnes yr^{-1} much of it in a dissolved and particulate organic form (e.g. amino acids) together with significant amounts of $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$ and $\text{NO}_2\text{-N}$. Although denitrification occurs within the sediments (e.g. Lok Tan and Rueger, 1979) and some of the fixed nitrogen is utilised within the marsh (e.g. Hanson and Gardner, 1978), export, though variable depending upon the particular marsh, is generally greater than the tidal input (e.g. Axelrad *et al.*, 1974; Teal and Valiela, 1978; Valiela *et al.*, 1978; Haines, 1979; Welsh, 1980). Thus the marshes studied by Axelrad *et al.* (1974) exported both particulate and dissolved organic carbon, the former being some 36–49% of the year's primary production. The contribution of other substances to coastal waters is relatively unknown, however, Hanson and Snyder (1980) found that little glucose was exported from a *Spartina alterniflora* marsh compared with that recycled within it.

It is, thus, becoming increasingly evident that salt marshes do act as regulators of nutrient concentration in and the suppliers of dissolved

organic phosphorus and nitrogen to coastal waters, thereby conditioning them for the inhabitants who utilise these substances. It should not, however, be forgotten that where the salt marshes are poorly developed or the river outflow is very large, the coastal waters receive substantial inputs directly from the catchment area. These substances may be inorganic (e.g. Maksimova *et al.*, 1978; Luoma and Cain, 1979; Rigler, 1979) or organic materials including leaves and peat. Even within the freshwater environment the organic particulates, which combined with associated micro-organisms may be considered as an "external rumen", are recognised as a major source of food in many lakes and streams (McLachlan, 1978), and in some Spanish estuaries, Gonzales (1975) considered that they contributed to the high productivity. While in the Arctic Ocean, the productivity of the coastal waters is dependent upon the supply of nutrients from the rivers (e.g. Alexander *et al.*, 1975) and detrital particles derived from beach vegetation and tundra banks (Broad, 1976). Accepting that one may distinguish, however incompletely, between the fluvio-terrestrial and the salt marsh additions to coastal waters, there is no clear attempt, in the literature, to evaluate the impact of the former upon the latter. Thus the nature of secondary metabolites derived from terrestrial sources, their concentrations and activities in river waters and their influence upon salt marshes is unknown, though their known biotic activity would suggest a fruitful field of investigation.

Recognition of the contribution of external metabolites made by these sources to the conditioning of coastal waters and the catalogue of their utilisation above gives no more than a general indication of the mechanism/s whereby such conditioning takes effect. In this respect the paper by Fontaine *et al.* (1978) is particularly interesting for it shows that as the usage of a spawning ground by herring decreased so too did the total amino-acid concentration. Curiously the concentrations of glycine, threonine, aspartic acid and serine increased. Of these, glycine apparently acted as an attractant to ophiuroid starfish which gradually replaced the ascidian population; serine is a known repellent of salmonids and both it and glycine apparently provide a stimulus to further change.

The ecology of red tides provides another insight into possible mechanisms, thus Petran (1977) found that a bloom of *Exuviaella cordata* was accompanied by an abundance of *Penilia avirostris* and *Acartia clausi*. While Honjo *et al.* (1978) found that water from a *Heterosigma* sp. red tide inhibited the growth of *Skeletonema costatum*, but not that of *Nitzschia closterium* and *Phaeodactylum tricorutum*; in the field, complete inhibition of *S. costatum*, *Chaetoceros* sp. and *Thalassiosira* sp., accompanied by a temporary decline of small flagellates was noted, on the other hand *Nitzschia* sp. was unaffected. Gauthier *et al.* (1978) investigating

the antibiotic activity of *Asterionella japonica* and *Chaetoceros lauderi* found that a chemical mediator released by *Prorocentrum micans* inhibited the synthesis of pigments and lead to a photoactivation of lipidic antibiotics.

Because red tide is so important, there is obviously great interest in possible means for its control. It has been found that dinoflagellates are sensitive to aponin a toxin produced by the blue-green alga *Gomphosphaeria aponina* (Kutt and Martin, 1975; Halvorson and Martin, 1980) and investigations of the mass culture and potential for use of *G. aponina* are now actively pursued (Eng-Wilmot and Martin, 1977a, b, 1979; McCoy *et al.*, 1979; Moon and Martin, 1979). Yet another insight comes from physiological and toxicity studies, thus the uptake of glucose by bacteria is influenced by the phosphate concentration (Overbeck and Toth, 1978) and the importance of humic materials in the speciation and availability of trace metals (e.g. Millward and Burton, 1975; Toleda *et al.*, 1980) has already been noted. While appreciating that the quality of fish diet cannot be compared directly with the influence of dissolved organic compounds, it is significant that Mehrle *et al.* (1977) found that the toxicity of D.D.T. to rainbow trout increased as the concentration of the amino acid methionine increased and conversely, the toxicity of dieldrin decreased; similarly the tolerance of channel catfish to toxaphene increased as the vitamin C concentration in the diet increased. On the other hand, Hodson *et al.* (1980) found that while lead toxicity and dietary deficiency of vitamin C in young rainbow trout produce the same symptoms, there was no metabolic interaction between the two.

To summarise, the hypothesis of Perkins (1977) has been substantiated to the extent that salt marshes do export substantial quantities of dissolved organic phosphorus and nitrogen compounds to coastal waters, and these result from the transformation of inorganic phosphorus and nitrogen compounds; were the marshes not present then these conditioning agents would, at least, be less abundant. Regarding, the mechanisms involved in maintaining ecological balance or inducing change, the work on *Gomphosphaeria aponina*, and its toxin aponin, indicates the manner in which change may be suppressed, on the other hand, the attractive effect of glycine upon ophiroid starfish shows how it may be promoted. One has therefore a glimpse of the underlying mechanisms whereby salt marshes may balance the quality of coastal waters and clearly there is an exciting prospect in this field. That the hypothesis is to some degree established by more recent work, serves only to emphasise the ill-advised nature of grandiose schemes of salt marsh reclamation.

There is a corollary to this argument which has a major significance. If the lay and scientific press are a fair indication, the promise of

biotechnology obscures the fact that substantial volumes of effluent must result. Nowhere in the clouds of heady euphoria surrounding these proposals can be seen much appreciation either that these arising will be biologically active or the necessity to project treatment and other needs for effective environmental management of these wastes. Yet the foregoing indicates clearly the need for forethought in these matters, and common prudence suggests involvement of waste and environmental management at an early stage, rather than learn once again the lessons of the past.

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